ABSTRACT - Regression estimates of genetic effects utilizing several specific population means from different generations. Keith H. Thompson, Cornell University.

A genetic experiment is conducted in which individuals are randomly selected from several populations and measured with respect to a quantitative characteristic. Two inbred diploid parents, P_1 and P_2, were used to generate the following populations: P_1, P_2, F_1, B_1, B_2, F_2, B_{11}, B_{12}, B_{21}, B_{22}, B_1selfed and B_2selfed. These populations differ in their expected genotypic distribution in predictable proportions, assuming that P_1 and P_2 differ at an arbitrary number of loci with respect to the quantitative characteristic measured.

Each genotype has associated with it an average phenotype or genotypic value which may be expressed in terms of certain defined genetic effects. For an arbitrary number of loci, say n, there are 3^n possible genetic effects which may be represented as independent linear functions of the 3^n genotypic values. The populations are composed of different proportions of these genotypes and thus have a predictable constitution in terms of mean genetic effects.

Within each population, however, similar genetic effects of like order have equal coefficients; hence it is necessary to estimate sums of like genetic effects instead of the effects themselves. For the twelve populations in this experiment, ten genetic effects are estimated. The multiple regression equation may be written as

$$\bar{P}' = XF'$$

where $\bar{P}=(\bar{P}_1,\bar{P}_2,\bar{F}_1,\bar{B}_1,\bar{B}_2,\bar{F}_2,\bar{B}_{11},\bar{B}_{12},\bar{B}_{21},\bar{B}_{22},\bar{B}_1s,\bar{B}_2s)$, $F=(\mu,h,dd,hh,ddh,hhh,d,dh,ddd,dhh)$, and X is a 12x10 matrix with rational coefficients. The solution $\hat{F}$ is now obtained by the method of least squares as

$$\hat{F}' = (X'X)^{-1}X'\bar{P}'$$

and exhibited.

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REGRESSION ESTIMATES OF GENETIC EFFECTS UTILIZING SEVERAL SPECIFIC POPULATION MEANS FROM DIFFERENT GENERATIONS

BU-123-M Keith H. Thompson, Cornell University November, 1960

An experiment is conducted in which randomly selected individuals from each of several genetic populations are measured with respect to a quantitative characteristic. In the particular experiment discussed here, two inbred diploid parents, P_1 and P_2, were used to generate the following populations: P_1, P_2, F_1, B_1, B_2, F_2, B_{11}, B_{12}, B_{21}, B_{22}, B_1 selfed, and B_2 selfed. It will be shown for these populations that a few limiting assumptions regarding the genetic model permit the estimation of certain defined genetic mean components.

Denoting the jth allele at the ith locus in both the maternal and paternal gametes as $A^i_{j_i}$, we may symbolically write the general genotype of a diploid individual heterozygous at n loci as

$$\prod_{i=1}^{n} A^i_{j_i} A^i_{k_i} \quad ; \quad j_i \neq k_i \text{ for all } i=1,\cdots,n \ .$$

In the simplest case where P_1 and P_2 differ by two alleles of a single factor; i.e., P_1 has genotype $A^1_1 A^1_1$ and P_2 has genotype $A^1_2 A^1_2$, the following genetic effects are defined:

$$\mu^1 = \frac{A^1_1 A^1_1 + A^1_2 A^1_2}{2} = \text{midparent value},$$

$$d^1 = A^1_2 A^1_2 - \mu^1 = \text{additive effect, and}$$

$$h^1 = A^1_1 A^1_2 - \mu^1 = \text{dominance effect.}$$

These effects may be expressed in matrix notation in terms of genotypes or their corresponding genotypic values as

$$E^1_1 = AG^1_1$$

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where E_1 represents the vector of effects (μ^1, d^1, h^1), G_1 represents the vector of genotypes $(A_1^1A_1^1, A_1^1A_2^1, A_2^1A_2^1)$, and A is a real-valued, non-singular, 3x3 matrix satisfying the above definitions. Thus,

$$\begin{pmatrix} \mu^1 \\ d^1 \\ h^1 \end{pmatrix} = \begin{pmatrix} \frac{1}{2} & 0 & \frac{1}{2} \\ -\frac{1}{2} & 0 & \frac{1}{2} \\ -\frac{1}{2} & 1 & -\frac{1}{2} \end{pmatrix} \begin{pmatrix} A_1^1A_1^1 \\ A_1^1A_2^1 \\ A_2^1A_2^1 \end{pmatrix}$$

and

$$\begin{pmatrix} A_1^1A_1^1 \\ A_1^1A_2^1 \\ A_2^1A_2^1 \end{pmatrix} = \begin{pmatrix} 1 & -1 & 0 \\ 1 & 0 & 1 \\ 1 & 1 & 0 \end{pmatrix} \begin{pmatrix} \mu^1 \\ d^1 \\ h^1 \end{pmatrix}$$

These definitions of effects for a single factor may now be used to extend the definitions to cover the case where P_1 and P_2 differ at an arbitrary number of loci. A symbolic multiplication notation (Robson, 1960) is useful in this respect to represent each of the higher order genetic effects as a symbolic product of single factor effects. It is also useful, as implied earlier, in representing a genotype of n factors as a product of single factor genotypes.

If the symbol "*" denotes Kronecker multiplication and "o" denotes symbolic multiplication, we define the vector of genetic effects for two loci as

$$\begin{aligned} E_1 * E_2 &= (\mu^1, d^1, h^1) * (\mu^2, d^2, h^2) \\ &= (\mu^1 o \mu^2, \mu^1 o d^2, \mu^1 o h^2, d^1 o \mu^2, d^1 o d^2, d^1 o h^2, h^1 o \mu^2, h^1 o d^2, h^1 o h^2) \\ &= (\mu, d_2, h_2, d_1, dd_{12}, dh_{12}, h_1, hd_{12}, hh_{12}) \quad . \end{aligned}$$

Similarly, the vector of genotypes for two loci may be obtained as

$$G_1 * G_2 = (A_1^1A_1^1, A_1^1A_2^1, A_2^1A_2^1) * (A_1^2A_1^2, A_1^2A_2^2, A_2^2A_2^2)$$

$$= (A_1^1A_1^1 \circ A_1^2A_1^2, A_1^1A_1^1 \circ A_1^2A_2^2, A_1^1A_1^1 \circ A_2^2A_2^2, A_1^1A_2^1 \circ A_1^2A_1^2, A_1^1A_2^1 \circ A_1^2A_2^2, A_1^1A_2^1 \circ A_2^2A_2^2,$$

$$A_2^1A_2^1 \circ A_1^2A_1^2, A_2^1A_2^1 \circ A_1^2A_2^2, A_2^1A_2^1 \circ A_2^2A_2^2)$$

$$= A_1^1A_1^1A_1^2A_1^2, A_1^1A_1^1A_1^2A_2^2, A_1^1A_1^1A_2^2A_2^2, A_1^1A_2^1A_1^2A_1^2, A_1^1A_2^1A_1^2A_2^2, A_1^1A_2^1A_2^2A_2^2,$$

$$A_2^1A_2^1A_1^2A_1^2, A_2^1A_2^1A_1^2A_2^2, A_2^1A_2^1A_2^2A_2^2) \quad .$$

The definitions of the 3^2 genetic effects in terms of the 3^2 genotypic values in the case where P_1 and P_2 differ at two loci may now be written as

$$E'_{(2)} = A_{(2)}G'_{(2)}$$

where $E_{(2)}=E_1 * E_2$, $A_{(2)}=A*A$, and $G_{(2)}=G_1 * G_2$.

For an arbitrary number of loci, say n, the 3^n possible genetic effects may be defined as independent linear functions of the 3^n genotypic values and written

$$E'_{(n)} = A_{(n)}G'_{(n)}$$

where $E_{(n)}=E_1 * \cdots * E_n$, $A_{(n)}=A * \cdots * A$, and $G_{(n)}=G_1 * \cdots * G_n$. Since $A_{(n)}$ is non-singular, any genotype may be expressed uniquely as a linear function of genetic effects since

$$G'_{(n)} = A^{-1}_{(n)}E'_{(n)}$$

where $A^{-1}_{(n)}=(A * \cdots * A)^{-1}=A^{-1} * \cdots * A^{-1}$.

The different populations generated by crossing the two inbred diploid parents, P_1 and P_2, differ in their genotypic distributions in predictable

proportions, and using the relation $G_1'=A^{-1}E_1'$, they also differ in the constitution of their mean genetic effects. In the simplest case again, where P_1 and P_2 differ at a single locus with respect to the quantitative variable measured, the different populations are genotypically constituted as

	$A_1^1A_1^1$	$A_1^1A_2^1$	$A_2^1A_2^1$
$P_1 = P_1$ selfed	1	0	0
$P_2 = P_2$ selfed	0	0	1
$F_1 = P_1 \times P_2$	0	1	0
$B_1 = F_1 \times P_1$	$\frac{1}{2}$	$\frac{1}{2}$	0
$B_2 = F_1 \times P_2$	0	$\frac{1}{2}$	$\frac{1}{2}$
$F_2 = F_1$ selfed	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$
$B_{11} = B_1 \times P_1$	$\frac{3}{4}$	$\frac{1}{4}$	0
$B_{12} = B_1 \times P_2$	0	$\frac{3}{4}$	$\frac{1}{4}$
$B_{21} = B_2 \times P_1$	$\frac{1}{4}$	$\frac{3}{4}$	0
$B_{22} = B_2 \times P_2$	0	$\frac{1}{4}$	$\frac{3}{4}$
B_1 selfed	$\frac{5}{8}$	$\frac{1}{4}$	$\frac{1}{8}$
B_2 selfed	$\frac{1}{8}$	$\frac{1}{4}$	$\frac{5}{8}$

and genetically constituted as

	μ^1	d^1	h^1
$\bar{P}_1$	1	$-\frac{1}{2}$	0
$\bar{P}_2$	1	$\frac{1}{2}$	0
$\bar{F}_1$	1	0	1
$\bar{B}_1$	1	$-\frac{1}{2}$	$\frac{1}{2}$
$\bar{B}_2$	1	$\frac{1}{2}$	$\frac{1}{2}$
$\bar{F}_2$	1	0	$\frac{1}{2}$
$\bar{B}_{11}$	1	$-\frac{3}{4}$	$\frac{1}{4}$
$\bar{B}_{12}$	1	$\frac{1}{4}$	$\frac{3}{4}$
$\bar{B}_{21}$	1	$-\frac{1}{4}$	$\frac{3}{4}$
$\bar{B}_{22}$	1	$\frac{3}{4}$	$\frac{1}{4}$
$\bar{B}_1$ selfed	1	$-\frac{1}{2}$	$\frac{1}{4}$
$\bar{B}_2$ selfed	1	$\frac{1}{2}$	$\frac{1}{4}$

For any particular population in any generation we may now represent its genotypic distribution and mean genetic effect constitution in matrix notation; for example,

$$P_1 = B_{P_1} G_1'$$

and

$$\bar{P}_1 = C_{P_1} E_1'$$

respectively, where $B_{P_1}=(1,0,0)$ and $C_{P_1}=(1,-1,0)$.

The genotypic distributions and mean genetic effect constitutions are easily extended as before to the case where P_1 and P_2 differ at n unlinked loci

by using a symbolic multiplication notation in conjunction with Kronecker products; for example,

$$P_1 = B_{P_1(n)} G'_{(n)}$$

and

$$\bar{P}_1 = C_{P_1(n)} E'_{(n)}$$

where $B_{P_1(n)} = B_{P_1} * \cdots * B_{P_1}$ and $C_{P_1(n)} = C_{P_1} * \cdots * C_{P_1}$. All of the populations may be similarly represented. Now, if we let $\bar{P} = (\bar{P}_1, \bar{P}_2, \bar{F}_1, \bar{B}_1, \bar{B}_2, \bar{F}_2, \bar{B}_{11}, \bar{B}_{12}, \bar{B}_{21}, \bar{B}_{22}$, $\bar{B}_1$ selfed, $\bar{B}_2$ selfed), we can write the mean genetic effect constitution of the populations collectively as

$$\bar{P}' = C_{(n)} E'_{(n)}$$

where $C_{(n)}$ is a 12×3^n matrix whose rows are $C_{P_1(n)}, \cdots, C_{B_{2s}(n)}$ in that order.

In the above set of non-independent equations, similar genetic effects of like order have equal coefficients within each population; hence it is necessary for estimation purposes to designate them by a sum notation. For example,

$$d = \sum_{i=1}^{n} d_i$$

$$h = \sum_{i=1}^{n} h_i$$

$$dd = \sum_{i<j} dd_{ij}$$

$$dh = \sum_{i \neq j} dh_{ij}$$

$$hh = \sum_{i<j} hh_{ij}$$

$$ddd = \sum_{i<j<k} ddd_{ijk}$$

$$\vdots$$

If we do this, $E_{(n)}$ is effectively reduced from a vector of 3^n components to one with $(n+1)(n+2)/2$ components. In the genetic problem where the number of factors affecting the quantitative character is unknown, it is necessary to assume n such that $(n+1)(n+2)/2$ is less than or equal to the number of independent populations available for estimation.

In the experiment under discussion twelve populations are available, and it is desired to estimate the sums of like genetic effects assuming that n=3. Obtaining $E_{(3)}$ as the Kronecker product of E_1, E_2, and E_3, we get

$$E_{(3)} = (\mu, d_3, h_3, d_2, dd_{23}, dh_{23}, h_2, hd_{23}, hh_{23}, d_1, dd_{13}, dh_{13}, dd_{12}, ddd_{123}, ddh_{123}, dh_{12}, dhd_{123}, dhh_{123}, h_1, hd_{13}, hh_{13}, hd_{12}, hdd_{123}, hdh_{123}, hh_{12}, hhd_{123}, hhh_{123}) .$$

We now define F_3, the reduced vector of summed components, as

$$F_3 = (\mu, h, dd, hh, ddh, hhh, d, dh, ddd, dhh) .$$

The order is chosen arbitrarily so that all components with an even number of d are grouped as the first six elements and those with an odd number of d are grouped as the last four elements. This arrangement is used for convenience in solving the resulting multiple regression equation, written as

$$\bar{P}' = XF_3'$$

where X is a 12x10 matrix with rational coefficients obtained easily from $C_{(3)}$. The set of equations is

$$
\begin{pmatrix} \bar{P}_1 \\ \bar{P}_2 \\ \bar{F}_1 \\ \bar{B}_1 \\ \bar{B}_2 \\ \bar{F}_2 \\ \bar{B}_{11} \\ \bar{B}_{12} \\ \bar{B}_{21} \\ \bar{B}_{22} \\ \bar{B}_1{}^s \\ \bar{B}_2{}^s \end{pmatrix} = \begin{pmatrix} 1 & 0 & 1 & 0 & 0 & 0 & -1 & 0 & -1 & 0 \\ 1 & 0 & 1 & 0 & 0 & 0 & 1 & 0 & 1 & 0 \\ 1 & 1 & 0 & 1 & 0 & 1 & 0 & 0 & 0 & 0 \\ 1 & \frac{1}{2} & \frac{1}{4} & \frac{1}{4} & \frac{1}{8} & \frac{1}{8} & -\frac{1}{2} & -\frac{1}{4} & -\frac{1}{8} & -\frac{1}{8} \\ 1 & \frac{1}{2} & \frac{1}{4} & \frac{1}{4} & \frac{1}{8} & \frac{1}{8} & \frac{1}{2} & \frac{1}{4} & \frac{1}{8} & \frac{1}{8} \\ 1 & \frac{1}{2} & 0 & \frac{1}{4} & 0 & \frac{1}{8} & 0 & 0 & 0 & 0 \\ 1 & \frac{1}{4} & \frac{9}{16} & \frac{1}{16} & \frac{9}{64} & \frac{1}{64} & -\frac{3}{4} & -\frac{3}{16} & -\frac{27}{64} & -\frac{3}{64} \\ 1 & \frac{3}{4} & \frac{1}{16} & \frac{9}{16} & \frac{3}{64} & \frac{27}{64} & \frac{1}{4} & \frac{3}{16} & \frac{1}{64} & \frac{9}{64} \\ 1 & \frac{3}{4} & \frac{1}{16} & \frac{9}{16} & \frac{3}{64} & \frac{27}{64} & -\frac{1}{4} & -\frac{3}{16} & -\frac{1}{64} & -\frac{9}{64} \\ 1 & \frac{1}{4} & \frac{9}{16} & \frac{1}{16} & \frac{9}{64} & \frac{1}{64} & \frac{3}{4} & \frac{3}{16} & \frac{27}{64} & \frac{3}{64} \\ 1 & \frac{1}{4} & \frac{1}{4} & \frac{1}{16} & \frac{1}{16} & \frac{1}{64} & -\frac{1}{2} & -\frac{1}{8} & -\frac{1}{8} & -\frac{1}{32} \\ 1 & \frac{1}{4} & \frac{1}{4} & \frac{1}{16} & \frac{1}{16} & \frac{1}{64} & \frac{1}{2} & \frac{1}{8} & \frac{1}{8} & \frac{1}{32} \end{pmatrix} \begin{pmatrix} \mu \\ h \\ dd \\ hh \\ ddh \\ hhh \\ d \\ dh \\ ddd \\ dhh \end{pmatrix}
$$

The solution $\hat{F}_3$ is now obtained by the method of least squares as

$$\hat{F}_3' = (X'X)^{-1}X'\bar{P}'$$

where $(X'X)$ is non-singular. The solution is numerically presented in the following steps:

$$(X'X) = \begin{pmatrix}
12 & 5 & \frac{17}{4} & \frac{25}{8} & \frac{3}{4} & \frac{73}{32} & 0 & 0 & 0 & 0 \\
5 & \frac{25}{8} & \frac{3}{4} & \frac{73}{32} & \frac{19}{64} & \frac{235}{128} & 0 & 0 & 0 & 0 \\
\frac{17}{4} & \frac{3}{4} & \frac{185}{64} & \frac{19}{64} & \frac{33}{128} & \frac{9}{64} & 0 & 0 & 0 & 0 \\
\frac{25}{8} & \frac{73}{32} & \frac{19}{64} & \frac{235}{128} & \frac{9}{64} & \frac{805}{512} & 0 & 0 & 0 & 0 \\
\frac{3}{4} & \frac{19}{64} & \frac{33}{128} & \frac{9}{64} & \frac{55}{256} & \frac{79}{1024} & 0 & 0 & 0 & 0 \\
\frac{73}{32} & \frac{235}{128} & \frac{9}{64} & \frac{805}{512} & \frac{79}{1024} & \frac{2875}{2048} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{17}{4} & \frac{3}{4} & \frac{185}{64} & \frac{19}{64} \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{3}{4} & \frac{19}{64} & \frac{33}{128} & \frac{9}{64} \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{185}{64} & \frac{33}{128} & \frac{2477}{1024} & \frac{85}{1024} \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{19}{64} & \frac{9}{64} & \frac{85}{1024} & \frac{79}{1024}
\end{pmatrix}$$

$$(X'X)^{-1} = \begin{pmatrix}
\frac{6,298,001}{754,135} & -\frac{68,082,082}{2,262,405} & -\frac{5,946,176}{745,135} & \frac{5,995,856}{150,827} & \frac{1,781,632}{754,135} & -\frac{40,901,216}{2,262,405} & 0 & 0 & 0 & 0 \\
-\frac{68,082,082}{2,262,405} & \frac{306,889,208}{2,262,405} & \frac{61,335,232}{2,262,405} & -\frac{33,100,256}{150,827} & -\frac{28,663,424}{2,262,405} & \frac{86,931,328}{754,135} & 0 & 0 & 0 & 0 \\
-\frac{5,946,176}{754,135} & \frac{61,335,232}{2,262,405} & \frac{5,964,096}{754,135} & -\frac{5,185,792}{150,827} & -\frac{1,796,352}{754,135} & \frac{34,397,696}{2,262,405} & 0 & 0 & 0 & 0 \\
\frac{5,995,856}{150,827} & -\frac{33,100,256}{150,827} & -\frac{5,185,792}{150,827} & \frac{63,297,664}{150,827} & \frac{2,880,768}{150,827} & -\frac{36,986,368}{150,827} & 0 & 0 & 0 & 0 \\
\frac{1,781,632}{754,135} & -\frac{28,663,424}{2,262,405} & -\frac{1,796,352}{754,135} & \frac{2,880,768}{150,827} & \frac{5,612,544}{754,135} & -\frac{19,981,312}{2,262,405} & 0 & 0 & 0 & 0 \\
-\frac{40,901,216}{2,262,405} & \frac{86,931,328}{754,135} & \frac{34,397,696}{2,262,405} & -\frac{36,986,368}{150,827} & -\frac{19,981,312}{2,262,405} & \frac{346,028,032}{2,262,405} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{430,306}{15,525} & -\frac{122,368}{1,725} & -\frac{424,576}{15,525} & \frac{89,824}{1,725} \\
0 & 0 & 0 & 0 & 0 & 0 & -\frac{122,368}{1,725} & \frac{120,512}{575} & \frac{118,528}{1,725} & -\frac{105,216}{575} \\
0 & 0 & 0 & 0 & 0 & 0 & -\frac{424,576}{15,525} & \frac{118,528}{1,725} & \frac{426,496}{15,525} & -\frac{85,504}{1,725} \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{89,824}{1,725} & -\frac{105,216}{575} & -\frac{85,504}{1,725} & \frac{114,688}{575}
\end{pmatrix}$$

$$(X'X)^{-1}X' = \begin{pmatrix}
\frac{211,095}{452,481} & \frac{211,095}{452,481} & -\frac{30,291}{452,481} & -\frac{313,350}{452,481} & -\frac{313,350}{452,481} & \frac{444,954}{452,481} & -\frac{485,406}{452,481} & \frac{60,582}{452,481} & \frac{60,582}{452,481} & -\frac{485,406}{452,481} & \frac{545,988}{452,481} & \frac{545,988}{452,481} \\
-\frac{1,349,370}{452,481} & -\frac{1,349,370}{452,481} & \frac{619,454}{452,481} & \frac{1,117,338}{452,481} & \frac{1,117,338}{452,481} & -\frac{1,232,838}{452,481} & \frac{2,430,782}{452,481} & -\frac{937,254}{452,481} & -\frac{937,254}{452,481} & \frac{2,430,782}{452,481} & -\frac{954,804}{452,481} & -\frac{954,804}{452,481} \\
\frac{3,584}{150,827} & \frac{3,584}{150,827} & \frac{7,168}{150,827} & \frac{98,768}{150,827} & \frac{98,768}{150,827} & -\frac{154,528}{150,827} & \frac{165,176}{150,827} & -\frac{14,336}{150,827} & -\frac{14,336}{150,827} & \frac{165,827}{150,827} & -\frac{179,512}{150,827} & -\frac{179,512}{150,827} \\
\frac{810,064}{150,827} & \frac{810,064}{150,827} & -\frac{793,104}{150,827} & -\frac{289,504}{150,827} & -\frac{289,504}{150,827} & \frac{646,848}{150,827} & -\frac{1,412,916}{150,827} & \frac{982,900}{150,827} & \frac{982,900}{150,827} & -\frac{1,412,916}{150,827} & -\frac{17,416}{150,827} & -\frac{17,416}{150,827} \\
-\frac{2,944}{150,827} & -\frac{2,944}{150,827} & -\frac{5,888}{150,827} & \frac{5,056}{150,827} & \frac{5,056}{150,827} & -\frac{45,440}{150,827} & -\frac{6,400}{150,827} & \frac{11,776}{150,827} & \frac{11,776}{150,827} & -\frac{6,400}{150,827} & \frac{18,176}{150,827} & \frac{18,176}{150,827} \\
-\frac{1,300,704}{452,481} & -\frac{1,300,704}{452,481} & \frac{2,225,056}{452,481} & \frac{30,432}{452,481} & \frac{30,432}{452,481} & -\frac{1,189,920}{452,481} & \frac{2,313,616}{452,481} & -\frac{2,036,880}{452,481} & -\frac{2,036,880}{452,481} & \frac{2,313,616}{452,481} & \frac{475,968}{452,481} & \frac{475,968}{452,481} \\
-\frac{382}{1,035} & \frac{382}{1,035} & 0 & \frac{813}{1,035} & -\frac{813}{1,035} & 0 & \frac{1,666}{1,035} & \frac{542}{1,035} & -\frac{542}{1,035} & -\frac{1,666}{1,035} & -\frac{3,312}{1,035} & \frac{3,312}{1,035} \\
\frac{256}{115} & -\frac{256}{115} & 0 & -\frac{304}{115} & \frac{304}{115} & 0 & -\frac{748}{115} & -\frac{356}{115} & \frac{356}{115} & \frac{748}{115} & \frac{736}{115} & -\frac{736}{115} \\
-\frac{128}{1,035} & \frac{128}{1,035} & 0 & -\frac{768}{1,035} & \frac{768}{1,035} & 0 & -\frac{1,696}{1,035} & -\frac{512}{1,035} & \frac{512}{1,035} & \frac{1,696}{1,035} & \frac{3,312}{1,035} & -\frac{3,312}{1,035} \\
-\frac{288}{115} & \frac{288}{115} & 0 & \frac{112}{115} & -\frac{112}{115} & 0 & \frac{784}{115} & \frac{688}{115} & -\frac{688}{115} & -\frac{784}{115} & -\frac{368}{115} & \frac{368}{115}
\end{pmatrix}$$

Thus, the least squares estimates of the genetic effects are represented as

$$\begin{pmatrix} \hat{\mu} \\ \hat{h} \\ \hat{dd} \\ \hat{hh} \\ \hat{ddh} \\ \hat{hhh} \\ \hat{d} \\ \hat{dh} \\ \hat{ddd} \\ \hat{dhh} \end{pmatrix} = (X'X)^{-1}X' \begin{pmatrix} \bar{P}_1 \\ \bar{P}_2 \\ \bar{F}_1 \\ \bar{B}_1 \\ \bar{B}_2 \\ \bar{F}_2 \\ \bar{B}_{11} \\ \bar{B}_{12} \\ \bar{B}_{21} \\ \bar{B}_{22} \\ \bar{B}_1{}^s \\ \bar{B}_2{}^s \end{pmatrix} .$$

Robson, D. S. 1960. Genetic and statistical theory for quantitative inheritance studies of haploids. Biometrical Genetics, p. 46-64, Pergamon Press, New York.